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EVOLUTION OF THE BASAL PLATES IN MONOCYCLIC CRINOIDEA CAMERATA

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PART III

EVOLUTION OF THE BASE IN MONOCYCLIC CAMERATA

I. EVOLUTION OF THE PENTAGONAL BASES

Having assumed that the anal plate plays no part in the evolution of the pentamerous base in the monocyclic Camerata, the succession of changes modifying this base may now be considered.

Starting with the simple pentagonal base *a—b—c—d—e—* (Fig. 9, No. 1), the first change noted is the reduction in number of basals from five to four. It is evident that this change is due to the anchylosis of but one pair of plates, either the anterior pair or occasionally in *Melocrinus* the sinistro-laterals. Accompanying this change there is usually a symmetrical reduction of the compound plate and an asymmetrical reduction of the adjacent basals. The formula for the base so developed is *a—b—cd—e—* (Fig. 9, No. 2) for the anterior anchylosis and *a—bc—d—e—* for anchylosis of the sinstro-laterals (Fig. 5, No. 2*a*). The next step is the reduction to three unequal basals by the anchylosis of two pairs of basals. In this combination the simple basal may be any one of the five primary plates, although the left- or right-anterior plate is usually the simple one. Anchylosis is here accompanied either by asymmetrical reduction of the compound plates on the side apposed to the simple basal or by deep-seated and symmetrical reduction. In either case the enlargement of the simple basal is usually symmetrical. Any of the three-basal forms might arise from any of the possible combinations of four basals, provided that the anchylosed pair in the four-basal form appears as one of the compound units in the three-basal form. Thus the four-basal form *a—b—cd—e—* might have given rise to a type in which either of the postero-lateral basals is free, as in *ea—b—cd—*, or *ab—cd—e—* The probabilities are, however, that the three-basal forms originated directly from the five-basal forms, without an intermediate four-basal stage. This succession is shown diagrammatically by changing formula *a—b—c—d—e—* to *ab—c—de—* for the *Platycrinus* type of base and to *ea—bc—d—* for the *Hapalocrinus* type of base (Fig. 9, Nos. 1, 3, and 4). Two-basal forms are not known in this succession, so the next stage is that of complete anchylosis (Fig. 9, No. 5). This change consists in the complete union of the basal plates, and may occur in either the five-, four-, or three-basal forms. The formula for complete anchylosis is *abcde.*

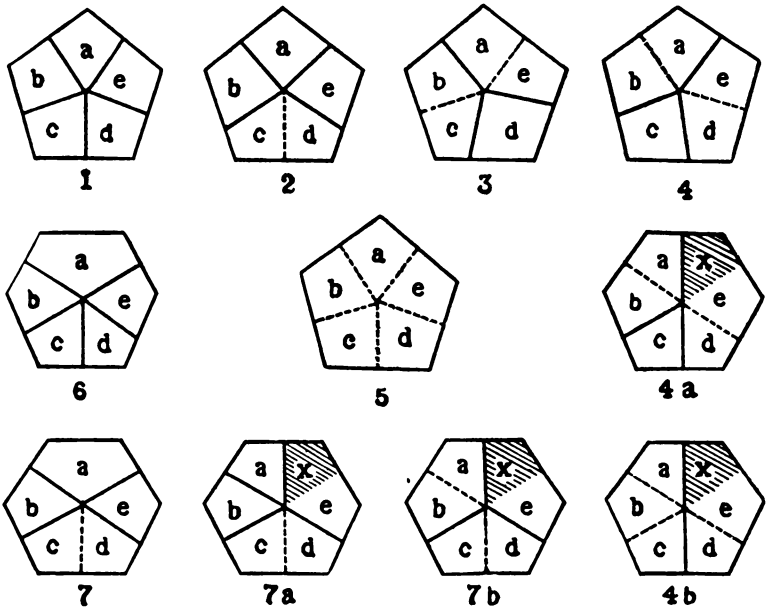

FIG. 9.—Diagrams illustrating the evolution of the base in the Camerata on the theory of atrophy and compensating hypertrophy: 1–5, combinations of the primitive five-basals; 1, 6, 7–7*b*, succession in the Batocrinidae; 1, 7*b*, succession in formation of the tripartite base in the Hexacrinidae; 1, 4–4*b*, succession in the formation of the bipartite base in the Hexacrinidae.

2. THEORIES FOR THE EVOLUTION OF THE BASE IN HEXAGONAL CAMERATA

a) *Enlargement of the posterior basal.*—Having in mind the time and place of development of the anal plate, let us examine the changes its introduction between the posterior radials would probably cause in the posterior basal in the cup of the primitive embryo. Since the zone of potential weakness caused by the enlarging hindgut is evidently in the right-posterior radius of the calyx, there can be but three possibilities for the enlargement of the posterior basal, which are: (i) normal symmetrical enlargement; (ii) enlargement through the anchylosis of a sixth basal factor appearing between the posterior and right-posterior basals; and (iii) enlargement through acceleration of growth in the right- or left-posterior sides.

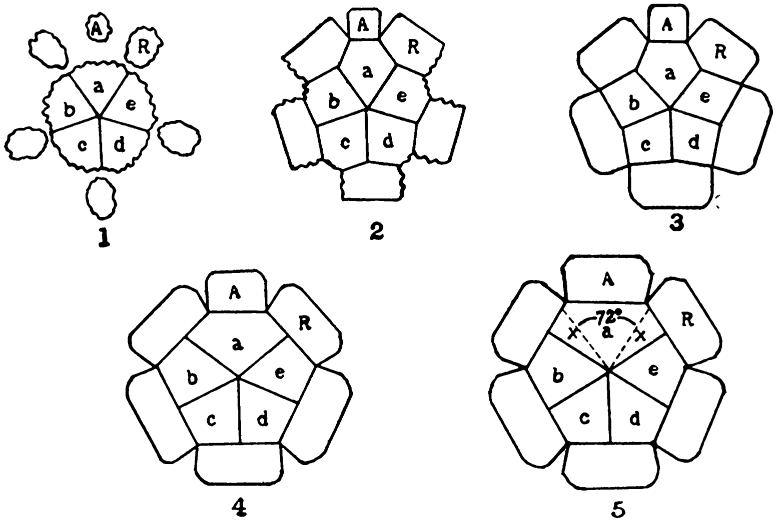

FIG. 10.—Diagrams illustrating modifications in shape and position of the basals and radials by the introduction of the anal plate; wavy lines indicate plate margins not in contact, smooth lines indicate plate margins in contact: 1–4, stages based upon the development of *Antedon;* 5, *Tanaocrinus* stage.

i. When the anal plate came into contact with the posterior basal (Fig. 10, No. 2), mutual trunkation of their apposed margins would take place, perhaps to a slight degree by absorption, but mainly from atrophy and broadening by lateral growth. As the radials and anal came into contact (Fig. 10, No. 3), growth pressure would cause a gradual spreading of the radial cycle at the posterior side, the lateral radials swinging outward and slightly forward (Fig. 10, No. 4), with a hinging motion along the lateral suture margins, until the anal plate reached its full proportionate size in development (Fig. 10, No. 5). The lateral basals, with their distal angles still in continuous growth-contact with the proximal ends of the radials, would separate slightly and gradually at their bases, as their longitudinal axes swung with the movement of the radials. The posterior basal would also move outward from the axial canal. These movements, however, are not migrational, but are of approximately the same type found in normal growth (see p. 502); for continuous growth along the plate margins, more rapid in the expanding areas than elsewhere, would keep the plate margins in continuous contact as in normal growth.

Since expansion by proximo-lateral growth is obviously not as rapid as by disto-lateral growth, the proximal ends of the basals would probably not be carried out from the center of the cup by growth pressure proportionately as far to the distal ends as they are in normal growth. Thus the proximal ends would apparently be lowered toward the horizontal plane of projection, and the projected angles of the proximal ends, which were 72° in the pentagonal base, would approach 60° in the hexagonal base. With greater expansion in the sarcode and greater plate growth taking place in the posterior region, the proximal angle of the enlarging posterior basal would increase, while those of the lateral basals would decrease through lengthening of their proximo-lateral margins by growth as well as by change in the angle of projection and shifting of their longitudinal axes. This method of basal change is symmetrical, normal, and apparently in keeping with the development in *Antedon* and the early monocyclic and dicyclic Camerata as we now know them.

The first expression of the pent-up energy in the developing intestine seems then to have been used up in a normal expansion of the posterior interray, which in this group proved to be a plane of weakness in the cup. Later, however, when the tendency for spreading was established, this energy was expressed in another direction, and in some of the modern crinoids (*Pentometrocrinus*, etc.) results in an almost complete flattening of the dorsal cup.

ii. The theory of the interpolation of a sixth basal factor to the right of the posterior basal is based upon the appearance of the radianal in that position in *Sagenocrinus*. It requires, first, the duplication of the posterior basal; secondly, the locking in of the sixth basal in the basal cycle; and, thirdly, closure of the posteriorly directed basal suture by anchylosis. On the ground of possibilities there can be no objection to this hypothesis, for we know that this certainly occurred in *Sagenocrinus*, nor can there be serious objection to the locking in of this plate in the basal cycle, for the radianal of *Pisocrinus* is locked in in the radial cycle. The most serious objection to this theory is that in the series of sutural reappearances in species with a hexagonal base a normal right-posterior basal suture has not been found, although the writer has made careful search for such examples.

iii. The theory of asymmetrical enlargement requires either enlargement of the left side of the posterior basal, or of the right side, which is Wachsmuth and Springer's theory for enlargement. In favor of the first development is the fact that in the Flexibilia Springer has found a general enlargement of the left side of the posterior basal.[1] In favor of the second part of this theory is the development to the right of the radianal in *Pisocrinus*, apparently in the face of the influence of the growing intestine which in the Flexibilia tends to carry this plate to the left of the right-posterior radial. The abundance of evidence Springer has brought in his work on Flexibilia far outweighs the slight evidence shown in *Pisocrinus* and inclines one to believe that factor x might have been added to left of basal a; but when we consider the evidence of increasing potency for distortion on the part of the intestine, there is a strong possibility that the intestine may have shoved the posterior basal to the left, as Wachsmuth and Springer believe, and may have at the same time inhibited the tendency of expansion on the part of the right-posterior basal, permitting the posterior basal to enlarge on the right side. We are here involved in a question of directive controls which cannot be readily answered, and, since the posterior basal in *Tanaocrinus* is symmetrically trunkated and developed, the writer is forced to the conclusion that asymmetrical development had not at that time appeared in the posterior basal.

The formula for a base developed upon the first theory is $\overline{xax}—b—c—d—e—$, or in shortened form $\bar{a}—b—c—d—e—$ (Fig. 9,

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[1] Ref. 31, p. 496.

No. 6); that of the second theory is *xa—b—c—d—e—*, while those of the third theory are $\overline{ax}$*—b—c—d—e—* for lateral enlargement of the left side, and *xa—b—c—d—e—*for lateral enlargement of the right side.

b) *Development of the quadripartite base.*—In the evolution of the four-basal, hexagonal base there can be no disagreement, as but one pair of basals, the anterior pair, is anchylosed. Anchylosis in this type of base is generally accompanied by symmetrical reduction of the compound plate and an asymmetrical and compensating enlargement of the apposed basals. The formula for the four-basal type, based upon the theory of symmetrical enlargement of the posterior basal, is $\bar{a}$*—b—cd—e—* (Fig. 9, No. 7); that of Wachsmuth and Springer, *xa—b—cd—e—* (Fig. 1, No. 7).

c) *Development of the tripartite base.*—In the discussion of the evolution of the tripartite base three theories will be considered: (i) the tortional theory of Wachsmuth and Springer; (ii) the bisection theory; and (iii) theory of atrophy and compensating hypertrophy.

i. Tortion theory: Wachsmuth and Springer's theory may be stated as follows: The equally tripartite base of the hexagonal Camerata originated from an unequally tripartite base of the *Platycrinus* type by the addition of an anal plate, which caused (1) a spreading of the posterior interradius; (2) a tortion of the base which brought the right-posterior and anterior basal sutures respectively into contact with the anal plate and the right-anterior radial; and (3) the addition of a lateral-growth factor (*x*), to the right of the left-anterior basal. The evolution of the base upon this theory may be expressed in formula as follows: *ab—c—de—* to *ab—cx—de—* (Fig. 1, Nos. 3, 9, 10).

Since this theory was thought to have been confirmed by an abnormal example of *Teleiocrinus umbrosus* in which the anal plate is missing and the base, supposedly, reduced to the *Platycrinus* type (*ab—c—de—*), it assumes (1) that the subequally tripartite base did not originate from the hexagonal five- or four-basal forms, but from another line, or (2) that it did originate from them and that an intermediate form existed in which the anal plate was temporarily lost·and the base was like that of *Platycrinus*. This latter assumption demands the loss of factor *x* and anchylosis of two pairs of plates in the five-basal form, as in changing *xa—b—c—d—e—*to *ab—c—de—*, or the factor *x*, the anchylosis of two pairs of plates, and the reappearance of the anterior suture in the four-basal form, as in changing *xa—b—cd—e—*to *ab—c—de—*. Bather in accepting[1] this theory apparently assumes an intermediate step, for in the generic discussion of *Abacocrinus*[2] he says: "From the imagined intermediate step [not from *Abacocrinus* itself], *Periechocrinus* may have been derived by fusion of 2 BB [*two basals*]."

In the review of the evolutional characteristics in the Batocrinidae and Actinocrinidae, we have seen that the anal plate first appeared in the five-basal form of the *ā—b—c—d—e—* type, and that it was probably introduced without other distortional changes than those assumed in the hypothesis here offered (see p. 667). In the four-basal form anchylosis of one pair of basals, the anterior pair, resulted. So far there have been no relative distortional shiftings of the basals or radials except in the posterior region.

Furthermore, there is not throughout the succession of Batocrinoidea and Actinocrinoidea a single species with the *ab—c—de—* type of base. Only in two similarly abnormal specimens, one of *Teleiocrinus umbrosus*, in the Springer collection, the other of *Steganocrinus pentagonus*, in the Walker Museum collection, is the unequally tripartite base belonging to the *ab—c—de—* group found. It does not seem possible, then, that in a succession so clearly outlined the anal plate should temporarily disappear in the imagined[3] intermediate form between *Abacocrinus* and *Periechocrinus*. The reversion and replacement herein implied are entirely out of harmony with the processes of evolution in crinoid development. Can it then be possible that the anterior suture reappeared in the intermediate form, so that shifting of the basals could take place, as believed by Wachsmuth and Springer? We know of no positive instances of the reversion of a phylogenetic trend by the appearance of such an atavistic feature as a new generic or specific character (see p. 544). Since there is apparently no hope along this line of development, let us start with the original *ā—b—c—d—e—* type of base, close the left-posterior and right-posterior sutures, and shift the plates in accordance with Wachsmuth and Springer's theory. We are here confronted at once with the fact that neither in *Antedon*, in the five-basal hexagonal forms of monocyclic or dicyclic Crinoidea, nor in the four-basal hexagonal Camerata, has any such shifting taken place. Since the stimulus for widening the posterior interradius has already accomplished its purpose, there is apparently no stimulating cause to accomplish such a shifting, and if there is no such stimulus, there is but one other alternative: the phylogenetic succession as emended by Bather[1] and accepted by Springer[2] is artificial.

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[1] Ref. 3, p. 427, third notice.

[2] Ref. 6, p. 166.

[3] Ref. 6, p. 166.

Grant for the moment that the succession as outlined is artificial, and starting with the ancestral form as proposed by Wachsmuth and Springer, develop the hexagonal, equally tripartite base from the pentagonal, unequally tripartite base. The anal plate being inserted as proposed, let us follow closely the steps required in the shifting of the basals. The posterior and left-posterior, the right-posterior and right-anterior basals have already anchylosed in pairs, which demands, as we have shown before, closed plate cycles. In order that the right-anterior compound basal *de* may assume a right-posterior position, as Wachsmuth and Springer have affirmed, sufficient expansion must take place between the radials and the basals to permit such shifting, or there must be absorption of the distal angle of this basal, the proximal angles of the radials, or of both coupled with inhibition of plate growth in order to permit their passing. At the same time that widening in the anal area is taking place there must be a compensating widening between the two anterior basals. This change demands a movement of the sarcode on the right side away from the anal plate in the radial cycle and toward it in the basal cycle, which is surely too remarkable a tortion to be deemed possible, especially in forms having the bilaterally symmetrical development shown in the camerate Crinoidea. Furthermore, this theory does not take into consideration the fact that it is the stimulus arising from the push of the rapidly developing intestine against the posterior interradius that has caused the introduction of the anal plate.

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[1] Ref. 6, pp. 159–70.

[2] Ref. 25, pp. 193–98.

Let us now turn to a study of the specimen of *Teleiocrinus umbrosus* (Pl. I, Nos. 1, 2, 4, 6) by which Wachsmuth and Springer thought their theory to have been confirmed. Upon careful examination of this specimen grave doubts have arisen in the writer's mind concerning the validity of its assigned orientation. *Teleiocrinus umbrosus* has a central anal tube; therefore use of this as a reference point for orientation is denied. If, however, we consider that the interray in which the abnormality (loss of the anal plate) occurred should perhaps show some variation from the supposedly normal interrays, a different answer to the problem is obtained. Four of the interrays in this specimen show the normal *Teleiocrinus umbrosus* type of development: 1, 2, 2, 2. The fifth interray shows the following arrangement: 1, 3, 4, 2, which varies from the normal posterior interray (*A*, 2, 3, 4, 2) or (*A*, 2, 4, 3, 2) by the loss of but two important plates—the anal plate and one plate of the superimposed pair. There is here too close a parallel to be considered entirely accidental, and it does not seem unreasonable that if some plates are missing from an interray, that interray should show signs of abnormality. If, then, it be assumed that the abnormal interray in this specimen of *Teleiocrinus umbrosus* is the true posterior interray, the basal formula is not *ab*—*c*—*de*—, as in *Platycrinus*, but *ab*—*cd*—*e*—, for the simple basal is bisected by the plane of the right-posterior interray.

Let us, before going farther, examine the specimen of *Steganocrinus pentagonus* (Pl. II, No. 15; Pl. III, Nos. 1, 2) which, like the specimen just described, has lost its anal plate. *Steganocrinus pentagonus*, unlike *Teleiocrinus umbrosus*, has a slightly eccentric anal tube; the vertical convexity of the posterior interray is much flatter than in the other interrays, and the interbrachial plates are ornamented at a lower level by low sharp nodes. If, then, this specimen be oriented according to the position of the anal tube, convexity of interrays, and ornamentation, the basal formula is found to be, not *ab*—*c*—*de*—, as in *Platycrinus*, but *b*—*cd*—*ea*—, for the simple basal is bisected by the plane of the left-posterior interray. In *Teleiocrinus umbrosus* the posterior basal has anchylosed with the left-posterior basal; in *Steganocrinus pentagonus* it is anchylosed with the right-posterior basal. The reversion herein implied is very close to being a solution for the problem of the appearance of the posteriorly directed basal suture, and we need no longer confuse the issue with origin from *Platycrinus* or other three-basal forms of the *ab—c—de—* type.

It seems then that Wachsmuth and Springer's theory for the development of the hexagonal, tripartite base does not meet the requirements of present needs, and we may turn to a discussion of the remaining theories.

ii. Bisection theory: Briefly stated, the bisection theory assumes that the posteriorly directed basal suture resulted from the bisection of the posterior basal in a quadripartite base, and anchylosis of the portions of the posterior basal to the adjacent basals. This development may be expressed in formula as follows: *ā—b—cd—e—* through *a—b—cd—e—a—* to *ab—c—d—ea—*. The first objection to this theory is that there are no known instances of the bisection of a growing plate in modern Echinodermata. The second objection is that in the examples of recurrence of sutures by delayed anchylosis there are no instances of the reappearance of a normal right-posterior basal suture when the posterior suture is present (see Pls. II, III), although the writer has, as previously stated, made careful search for such examples. This theory and any theory based upon the assumption of plate splitting as a phylogenetic characteristic may apparently be abandoned as a factor in the development of Crinoidea.

iii. Theory of atrophy and compensating hypertrophy: The theory of atrophy and compensating hypertrophy is that the posteriorly directed basal suture and the subequally tripartite base of the hexagonal, monocyclic typical Camerata arose from the atrophy of the right half of the enlarged posterior basal, a compensating enlargement of the right-posterior basal, and the anchylosis of the posterior and left-posterior basals.

This theory is based upon (1) the general presence of atrophy in the right side of the posterior basal in Flexibilia; (2) the non-appearance of the right-posterior basal suture in the specimens showing reappearance of lost sutures through delayed anchylosis, and (3) evidence showing the derivation of *Dichocrinus* from *Platycrinus* stock.

In speaking of the base in the Flexibilia, Springer says:

> The posterior basal upon which it [the anal series] rests is excavated into a sort of shallow socket, like the articulating face of a radial, on the right shoulder of the plate, so that we will usually see a small tongue or angle of that plate rising up to the left of the base of the anal plate higher than to the right; or, if the socket-like excavation is not so plain as this, the upper edge of the basal is distinctly sloped to the right.[1]

Furthermore, in *Abacocrinus* the writer has found a marked reduction of the right side of the posterior basal and a compensating enlargement of the right-posterior basal (Pl. II, No. 7). There is here shown a marked tendency for the stimulus arising from the developing intestine to inhibit the growth of the posterior basal upon the right side and to permit the growth of the adjacent right-posterior basal.

Upon two of the accompanying plates (Pls. I, II) are illustrated the specimens upon which the evidence for sutural reappearance through failure of anchylosis is based. These illustrations show clearly the appearance of the anterior suture in *Melocrinus*, *Actinocrinus*, *Steganocrinus*, and *Hexacrinus*, and this suture is so often represented that it cannot be ascribed to any other cause. The appearance of this suture could only be accounted for upon Wachsmuth and Springer's theory by plate splitting, a supposition which is absolutely without foundation. It will furthermore be noticed that in no instance do the posterior and right-posterior sutures appear in the same specimen. Both sutures are sometimes absent, but in general the posterior suture is present and the right-posterior absent. The reappearance of the anterior suture and the failure of the right-posterior suture to reappear in any specimen in which the posteriorly directed suture is present, and in which other combinations of lost and normal sutures do appear, is the evidence upon which the theory of atrophy and compensating hypertrophy is based, and is here submitted as evidence that plate shifting such as Wachsmuth and Springer assumed probably did not take place, but that the right-posterior basal suture assumed a posterior position upon partial atrophy of the posterior basal and compensating hypertrophy of the left side of the right-posterior basal. The formula of the tripartite, hexagonal base, upon the theory of atrophy and compensating hypertrophy, is *ab—cd—ex—*.

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[1] Ref. 31, p. 496.

The explanation of the reversion implied in the abnormal specimens of *Teleiocrinus umbrosus* and *Steganocrinus pentagonus* may upon this theory be readily explained. Upon loss of the anal plate, stimulus for shifting the posterior basal suture was also lost, but the tendency for anchylosis of the anterior basals established in the early Batocrinoidea was not changed. Anchylosis then took place in as nearly normal a manner as possible, one of the postero-lateral sutures only in each specimen failing to close.

It will be noted that in the preceding discussion no mention has been made of the proportionate amount of growth in the radials, the anal, and the enlarged basals. This is because some misconception has arisen concerning their development, owing to the assumption that the basal outline is a regular hexagon. From careful measurements of the proximal diameter of the radials and anal in over five hundred specimens of Batocrinidae and Actinocrinidae it was found that in general the largest plates in the radial cycle are the antero-lateral radials, while the postero-laterals or the anal are the smallest in the radial cycle. Since the posterior radials are reduced by the interpolation of the anal plate (see p. 549) and the margins of the posterior basal do not extend beyond the center of these radials, it is evident that the posterior basal did not enlarge to a width equal to that of two of the other basals, as Wachsmuth and Springer have assumed, nor is the base a regular hexagon. The reduction of the posterior basal and the compensating enlargement of the right-posterior basal do not then require a formidable amount of plate readjustment, especially when we remember what readjustments have taken place in *Pisocrinus* (see p. 535).

3. EVOLUTION OF THE BASE IN THE HEXACRINIDAE

The evolution of the base in the Hexacrinidae is not as simple a problem as the evolution of the base in the Batocrinidae, for the phylogenetic succession is not as clearly defined. The general affinities of the Hexacrinidae are with the Platycrinidae, but the paths of evolution resulting in the subequally tripartite and bipartite bases are obviously so different that it is better to consider their basal developments separately.

a) *Evolution of the tripartite base.*—As the evolution of the tripartite base in the Hexacrinidae has resulted in essentially the same type of base as in the Batocrinidae, the same theories of descent will be considered; these are Wachsmuth and Springer's theory of torsion, and the theory of atrophy and compensating hypertrophy.

i. Torsion theory: Wachsmuth and Springer's theory for the evolution of the tripartite, hexagonal base of the Hexacrinidae is: Upon interpolation of the anal plate in some form having the *Platycrinus* type of base (*ab—c—de—*), spreading of the radial cycle at the posterior side was accompanied by a spreading of the basal cycle at the anterior side, thus causing the compound, dextrolateral basal to shift so that the right-posterior suture came into contact with the anal plate, and the anterior suture into contact with the right-anterior radial, while at the same time compensating growth of the left-anterior basal filled the vacant space. This metamorphosis may be shown diagrammatically by changing formula *ab—c—de—* to *ab—cx—de—* (Fig. 1, Nos. 3, 9, 10). The method of development is the same as was postulated by Wachsmuth and Springer for the development of the base in the Batocrinidae and the same objections are in force, but as the relationship of the three-basal Hexacrinidae is apparently with the Platycrinidae, these objections will be reconsidered.

The strongest objection to the torsion theory is that the stimulus for widening the posterior interradius is due directly to the oblique pressure of the growing hind-gut upon the right-posterior radius and posterior interradius, and cannot therefore produce a spreading between the anterior basals. The second objection is that in the two cases of sutural reappearance, by delayed anchylosis, in *Hexacrinus* (Pl. III, Nos. 5, 6) the right-posterior suture does not appear, although in the specimen (Pl. III, No. 5), showing the reappearance of the left-posterior sutures it would naturally be expected. Wachsmuth and Springer's theory does not then seem entirely adequate in explaining the formation of this base, and we may consider the second theory.

ii. Theory of atrophy and compensating hypertrophy: This theory has been fully considered in the preceding discussion of the formation of the tripartite base in the Batocrinidae and need not be restated. It requires the interpolation of an anal plate in the radial cycle, partial atrophy of the right half of the posterior basal, a compensating enlargement of the right-posterior basal to bring the right-posterior basal suture into contact with the anal plate, and perhaps the closure of one or more of the primary sutures. However, when this theory is applied to the supposed phylogenetic succession resulting in the Hexacrinidae, a peculiar difficulty is encountered. The *Platycrinus* type of base (*ab—c—de—*) in changing to the subequally tripartite base (*ab—cx—de*) demands upon this theory the reappearance of the right-anterior basal suture. Sutural reappearance as a phylogenetic character is, however, not considered a probability, and the second theory also seems inadequate to meet the demands of this problem. There is, however, another phase of the problem which must not be overlooked, and that is the possibility that *Hexacrinus* and *Arthrocantha* did not originate from one of the Platycrinidae with an *ab—c—de—* type of base. This suggestion is not to be considered as a means of confusing the issue and saving the writer's hypothesis; it is inserted to call attention to the fact that there is practically nothing known about the ancestors of the Platycrinidae nor the predecessors of the Silurian genera belonging to that family. The evidence derived from sutural reappearance by delayed anchylosis in the Batocrinidae and Hexacrinidae is such that there seems to be but one possible conclusion to be drawn, which is that *Hexacrinus* and *Arthrocantha* probably originated, not from a three-basal form of the *ab—c—de—* type, but from a simple five-basal type. The changes required in the suggested line of descent consist of: interpolation of the anal plate by portional migration; closure of the anterior and left-posterior basal sutures; partial atrophy of the posterior basal; and compensating hypertrophy of the right-posterior basal to shift the right-posterior suture to a posterior position (Fig. 9, Nos. 1, 7*a*, *b*).

b) *Evolution of the bipartite base.*—Wachsmuth and Springer's theory[1] for the origin of the bipartite, hexagonal base is stated as follows: "The bipartite base is probably derived from the tripartite, which preceded it in time, and *x*, which in the latter constituted a part of *c*, is united with *de*, and *ab* with *c* [Fig. 1, Nos. 11, 12]." Thus upon the shifting of plate *de* the tendency for the enlargement of plate *c* was inhibited, and a compensating growth of plate *de* filled the space formerly filled by the enlargement of plate *c*. This metamorphosis is shown by changing formula *ab—cx—de—* to *abc—xde—*.

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[1] Ref. 39, p. 56.

To this theory, however, there are the same objections that were encountered in that of the formation of the tripartite base in both the Batocrinidae and the Hexacrinidae. Torsion such as is assumed for the shifting of the compound plate *de* is apparently impossible, as the stimulus for enlarging the posterior interradius is due to the pressure from the growing hind-gut and cannot affect the anterior basal sutures. Furthermore, the examples of suture reappearance in the bipartite base show the potential presence and position of all but the right-posterior suture (Pl. III, Nos. 8, 9, 10). Wachsmuth and Springer's theory again does not seem adequate to explain the changes which have taken place and we may consider the theory of atrophy and compensating hypertrophy.

When the theory of atrophy and compensating hypertrophy, which has been thoroughly discussed, is applied to the phylogenetic succession as formulated by Wachsmuth and Springer, it also meets with the same trouble that was encountered in considering the evolution of the tripartite base. In this case the anterior basal suture must reappear as a phylogenetic character. Phylogenetic reappearance of a suture lost through anchylosis is, however, considered impossible, and the phylogenetic succession as postulated by Wachsmuth and Springer must be examined.

There are, it is true, many similar characteristics in the Hexacrinidae having tripartite and bipartite bases, but when the tegminal structures of the *Hexacrinus* and *Dichocrinus* are compared there is a marked difference. *Hexacrinus* has a ridged tegmen composed of medium-sized plates, and the ambulacrals are usually partially incorporated. *Dichocrinus*, however, has in its earliest expression in the Kinderhook a flexible tegmen composed of minute interambulacrals and unincorporated ambulacrals. *Dichocrinus* therefore apparently could not have originated from the

Devonian expression of *Hexacrinus*, as the reversion from a camerate type of tegmen to the flexible type, and a redevelopment of the camerate type as shown in later forms of *Dichocrinus* and more strongly in its descendants, *Talarocrinus*, etc., are scarcely probable. When, however, *Dichocrinus* (Pl. III, Nos. 12, 15) is compared with a Kinderhook species of *Platycrinus*, namely *P. symmetricus*, (Pl. III, Nos. 13, 14), such a remarkably close parallel in calyx structure is noted that with the insertion of an anal plate and proper modification of the base *P. symmetricus* could scarcely be distinguished in calyx structure from *Dichocrinus inornatus*. However, some species of *Dichocrinus* have uniserial arms, and all have a circular stem. *Dichocrinus* could not then have originated from the immediate ancestor of *P. symmetricus*, but from a somewhat earlier stage where the stem was circular, the arms uniserial, and the base of the *ab—c—de—* type. Hence a new theory for the origin of the bipartite, hexagonal base is suggested:

Dichocrinus and its descendants probably originated from some genus of the Platycrinidae which had a circular stem, flexible tegmen, branching uniserial pinnulate arms, and a base of the *ab—c—de—* type. The hexagonal, tripartite base originated by interpolation of the anal plate in the radial cycle by portional migration, closure of the left-anterior suture, partial atrophy of the right side of the posterior basal, and a compensatory hypertrophy of the left side of the right-posterior basal which shifted the right-posterior basal suture to a posterior position. This metamorphosis is expressed in changing formula *ab—c—de—* to *abc—dex—* (Fig. 9, Nos. 4, 4*a*, *b*).

4. THE SUCCESSION OF BASAL CHANGES IN THE PLATYCRINIDAE AND THE HEXACRINIDAE

The succession of basal changes in the Platycrinidae and the Hexacrinidae seems, from the evidence herein offered, to have followed a different line from that postulated by Wachsmuth and Springer, and the following succession is suggested.

The earliest Platycrinidae, as shown by the ontogenetic development of *Platycrinus*, had a simple pentagonal base of the *a—b—c—d—e—* type and a circular stem. Before the Niagaran (Silurian) this genus gave rise to the *Platycrinus* type of base (*ab—c—de—*)

in *Coccocrinus*, etc., and to the *Stephanocrinus* type of base (*ea—bc—d—*) in *Hapalocrinus*. Anchylosis of the basals in these forms was accompanied by reduction of the compound plate either by superficial or by deep-seated atrophy, and compensating hypertrophy of the simple basal. From *Coccocrinus* two lines of descent seem to have originated: the one culminating in *Platycrinus*, etc., with the *ab—c—de—* (Fig. 9, No. 4) type of base and an elliptical stem; the other culminating in *Dichocrinus* with its hexagonal, bipartite base (*abc—dex—*) (Fig. 9, No. 4*b*) and a circular stem. Interpolation of the anal plate in Dichocrinus is marked by reduction of the posterior radials, and the base is not a regular hexagon. The origin of the hexagonal genera with the tripartite base *ab—cd—ex—* (Fig. 9, No. 7*b*) is doubtful, but they were probably derived from an early branch of the primitive Platycrinidae, in which the base was a simple pentagon of the *a—b—c—d—e—* type and the stem circular.

SUMMARY OF CONCLUSIONS

In the preceding discussion the writer has attempted to portray the various stages of development through which the basal plates of the monocyclic Camerata have passed, and to explain the processes by which these results were obtained. Many of the theories herein set forth will undoubtedly be modified by the discovery of new evidence, and this study is offered merely as a working hypothesis upon which, perhaps, a stronger classification of the Crinoidea may be erected. As a result of this study the following conclusions have been reached:

1. The ancestor of the monocyclic Camerata was a simple, generalized crinoid with pentamerous symmetry.

2. The base of the pentagonal Camerata is not the result of reversion from an intermediate hexagonal stage, but is in a primitive condition as far as influence of the anal plate is concerned.

3. The anal plate is of secondary origin, and originated by primary interpolation between the latero-distal margins of the posterior radials.

4. The hexagonal base of the monocyclic Camerata resulted from the separation of the posterior radials and trunkation of the

posterior basal by the anal plate, the anal plate having been interpolated by portional migration in the space created by the demand of the hind-gut for enlargement.

5. The widening of the posterior basal upon interpolation of the anal plate was bilaterally symmetrical.

6. The quadripartite, hexagonal base resulted from the anchylosis of the anterior pair of basals in a hexagonal genus with a pentapartite base.

7. The posteriorly directed basal suture in the subequally, tripartite and bipartite, hexagonal bases is the homologue of the right-posterior basal suture in the pentapartite and quadripartite bases, which has shifted its position through atrophy of the right half of the posterior basal and a compensating hypertrophy of the left side of the right-posterior basal.

8. The basal sutures lost through anchylosis are potentially present in the basal cup, and liable to reappear in individual cases of delayed anchylosis, but not as a phylogenetic character.

9. The tripartite, hexagonal base in the Batocrinidae resulted from the appearance of the posteriorly directed basal suture (see 7) in a quadripartite base, accompanied by closure of the anterior and left-posterior basal sutures.

10. The hexagonal, tripartite base of the Hexacrinidae resulted from the interpolation of an anal plate by portional migration, through shifting of the right-posterior basal suture to a posterior position, and closure of the anterior and left-posterior basal sutures, in a simple platycrinid with a pentapartite base.

11. The bipartite, hexagonal base in the Hexacrinidae resulted from interpolation of the anal plate by portional migration, shifting of the right-posterior basal suture to a posterior position, and closure of the right-anterior basal suture, in a platycrinid with a pentagonal, unequally tripartite base.

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